COLLECTIVE TERRITORIES IN GALÁPAGOS MOCKINGBIRDS, WITH NOTES ON OTHER BEHAVIOR¹

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OLLECTIVE territories do not fit easily into the more usual categories of territoriality (e.g., Hinde, 1956) and the few cases described for birds demonstrate a variety of forms. In the evolution of social behavior in the Crotophaginae, one of the six subfamilies of cuckoos, the defense of colonial territories coincides with the reduction or disappearance of territorial defense by the pair, which has permitted communal nesting (Davis, 1942). In contrast, the Jackdaw (Corvus monedula) and Rook (C. frugilegus) both defend, albeit not very rigorously, colonial territories within which they feed, but also maintain pair territories around the nest. Coveys of quail (Lophortyx californica) outside the breeding season do not defend a particular area but familiarity with the area is important in determining the initial dominance of aliens by resident birds (Howard and Emlen, 1942). Carrick (1963) describes a particularly interesting situation in the Australian Magpie (Gymnorhina tibicen) in which territorialism and associated social and sexual interactions limit breeding to about one-quarter of the adult population, these breeding birds being among those in small social groups (each of two to ten birds) that live permanently within territories of five to 20 acres. In no other species has the nature of the reserve of nonbreeding birds been distinguished so clearly (cf. Hensley and Cope, 1951, who found a large but usually invisible reserve). The mockingbirds described below defend collective territories within which they feed and roost but intensive observations were not made during the breeding season.

Apart from the ubiquitous finches the mockingbirds are among the most obvious of the small land birds of the impoverished Galápagos avifauna. They have been considered sufficiently distinct from other mockingbirds (*Mimus*, spp.) to be placed in a separate genus, *Nesomimus*. Within the archipelago this genus shows considerable variation: no island has more than one form but the forms on Chatham (San Cristóbal), Hood, and the islets near Charles (Floreana) are so different from each other that they are described as separate species, and Swarth (1932) divides the fourth species into seven races that occur on most of the other islands.

The behavior of the Galápagos mockingbirds was first studied by Venables (1940) who found N. melanotis on Chatham Island to be strongly territorial while breeding. In particular he describes a form of aggressive territorial

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display which he calls "posture dancing" and a "branch chase" which may be sexually motivated. Both of these displays are considered again below.

METHODS

During 1962–63 I spent about three months on the Galápagos Islands and had occasion to watch the mockingbirds on several islands. Most of the observations reported here were made from 12–28 December 1962, on Hood Island where N. macdonaldi is numerous and particularly tame. Shorter visits were made to Tower Island (22–24 November, 4–8 January) and Champion Islet (near Charles) 11–15 January. Intervening periods were spent at Indefatigable Island (Santa Cruz). In many cases the birds were caught, usually in mist nets, and marked with colored plastic legbands. On some occasions identifications were based on plumage characters.

On Hood Island our camp was about two miles east of Punta Cevallos on the north shore at the eastern end of the island on a small triangular patch of sand between the bank of rounded lava boulders that fringes the sea and the thorny shrub characteristic of the island. Immediately upon our arrival we were "taken over" by the resident "band" of mockingbirds that were a constant source of delight to us with their boundless curiosity. Their tameness meant that it was little trouble to catch them in mist nets (or by hand in the cooking pots) and I marked a total of 21 birds at various places near the camp. Most of the observations were made on these birds, in the course of other work. In addition I watched some of the mockingbirds on the south coast for short periods and marked four of these.

RESULTS OF MARKING

On Hood Island the mockingbirds on the north shore characteristically occurred in groups that I have called "bands." Of the 21 birds marked near our camp, six comprised the band that occupied the campsite (called RW's band after the color combination of the dominant member). Eight formed RR's band to the east of the camp. Of seven marked birds in these two bands, three were rarely or never seen again, two were in a band of seven to the west and two formed the band to the south of the campsite.

None of these mockingbirds showed the spotted breast characteristic of young ones (Swarth, 1931), nor did they have the yellow gape and buff-colored rump that I saw on young N. parvulus on Indefatigable Island. Every bird was in worn plumage; the tails were so worn that measurements were difficult to evaluate but the 20 wing measurements fall clearly into two groups which fit well with Swarth's (op. cit.) nonoverlapping measurements for males

and females. In the two bands there were eight males (of which six were heard to sing) and six females.

OBSERVATIONS OF BEHAVIOR

Each of the two bands of mockingbirds (RW, RR) studied closely occupied a restricted area within which they fed and roosted; this situation seemed to apply elsewhere near the coast, but in the more arid interior of the island the mockingbirds occurred in twos, or less often threes or fours, and during my brief visits I saw little territorial behavior. On the windswept treeless southern coast of the island amongst the nests of boobies (Sula nebouxii and S. dactylatra), frigatebirds (Fregata minor), and albatrosses (Diomedea irrorata) the mockingbirds appeared not to form discrete bands and to lack the obvious dominance hierarchy of RW's band. For much of the time the members of a band moved around together in a widely scattered group. Occasionally (six or more observations) a single alien bird furtively crossed a territorial boundary only to be driven off by one or more of the residents (nos. 1, 2, 4, and 6 were observed chasing intruders). The structure of these bands and the relations between bands are described below.

Intragroup behavior.—On Hood Island the mockingbirds are particularly noisy and the most noticeable behavior within the band is a display which resembles the begging of young birds. It is given by both males and females to dominant members of either sex. The crouched posture is accompanied by a raucous squeak (Fig. 1) and is apparently a sign of submission. Very frequently the submissive bird turns its back on the dominant individual. Occasionally this submissive posture is given in response to the call of a dominant bird up to 20 yards away. In feeding situations there was a linear dominance hierarchy, demonstrated by "Begging" to all higher birds, except that in RW's band (at least) no. 2 did not beg to RW (no. 1) but gave a faint rattle call instead; between nos. 2 and 3 there was no begging and it was as if they were equal. I never saw a Begging bird being fed, but at least twice the dominant bird pecked in a slow, hesitant manner at the open beak. Bryan Nelson writes (in litt.), "... if a dominant individual is trying to dispel another bird from, say, a source of food it uses (or may use) a quite distinct form of pecking, which is essentially that used to hoist heavy twigs or stones aside, when feeding." I never recorded this kind of pecking possibly because it only occurs commonly amongst larger, probably unstable, groups of mockingbirds. A silent running chase in which the wings were slightly drooped occurred frequently, and occasionally ended with the chaser (male) attempting to peck the nape of the chased (female?). This is Venables's "branch chase" except that I usually saw it on the ground. This type of chasing was



Fig. 1. Begging Display. The bird on the right has just arrived and is dominant to the bird on the left. (Photo by R. W. Risebrough.)

mostly seen between 1, 3 and 5, 6, suggesting that they were pairs, but I saw no copulation. Dominant birds also chase squawking subordinates. I could detect no differences in the dominance of individuals in different parts of the group territory, but I did not set up feeding stations or watch extensively at distant sites. Some of the interactions within RW's band during 0600–1200 hours on 15 December 1962 are recorded in Table 1.

Of the members of RW's band, RW and no. 3 sang each day in occasional short bursts, preferring different song posts. Song was twice heard briefly from no. 5, the only other male in the band. On five occasions mockers (two then unmarked, once RW, twice no. 5) were seen to carry a twig to two uncompleted nests in bushes. Three of RR's band sang (two birds with the measurements of males were not heard to sing).

J. B. Nelson (in litt.) considers that the mockingbirds at Punta Suarez recognized each other by their facial patterns; frequently "before attacking, a bird would run round or stretch round and peer into the face of the other as though it was uncertain of the other's identity." In this region the bands apparently number up to 40 individuals which may account for this un-

TABLE 1

Subordinate individual	Sex	Dominant individual					
		RW	RBk	PM	ОВ	BY	OG
RW	ð	_					
RBk	8	B, (C)					
PM	2	(R)	(R?)	_			
OB	9		B, C	B, C			
BY	8	В	4B, C	2B, 2C	2B, (C)	_	
OG	2	В	В	С	(C)	C, 2R	_

The majority of interactions that occurred between dawn and 1200 h on 15 December 1962 are included. Parentheses indicate interactions observed on other days. B=Begging-squawk. C=Chase and squawk. R=Silent running-chase.

certainty, for I saw little behavior that could be explained in this way amongst the bands of six and eight that I watched closely near Punta Cevallos.

Intergroup behavior.—On Hood Island Dancing occurred whenever two bands met, but this was infrequent. Usually it was initiated by the dominant members of the bands and often spread to all the others nearby so that ten birds might be posturing at each other. I never saw two lone individuals Dancing (except once on Tower Island). It seemed to me that one band was opposing the other and it was not merely "other birds attracted by the spreading excitement and by their natural curiosity." as suggested by Venables (1940) for N. melanotis. The Dancing occurred at the boundary of the collective territory (Fig. 2) and presumably the display serves to delimit this boundary. The form of the dance is rather similar to the Dancing of Mimus polyglottos which is described in detail by Hailman (1960) except that flicks of the tail and wings are more pronounced. Ranged on either side of an imaginary line the birds make a series of forward, backward, or lateral steps following and keeping within about three feet of each other and often almost touching. Each jerky step is accompanied by a flick of the wings and followed by an exaggerated upward flip of the unspread tail. The tail-flip sometimes included some lateral movement also. The characteristic posture during this display is an upright one with the body tall and thin, but this is usually alternated with a head-forward position sometimes with feathers fluffed (presumably betokening a more aggressive tendency). The head-up posture is more often accompanied by a step back or sideways and the head-forward posture by a step forward. Dancing is often accompanied by various calls, some are squawks probably given by non-dancers in response to the other calls. On the few occasions I saw single birds chased from a territory, these were never the dominant members of a foreign band.

The mockingbirds in the seabird colonies on the south coast were often in groups but I found no evidence of territorial behavior and I never saw a

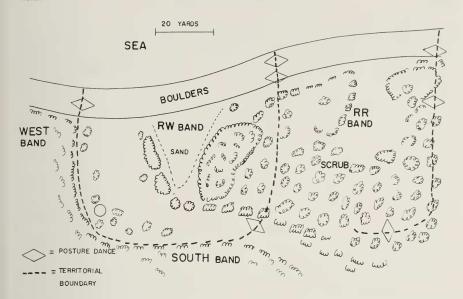


Fig. 2. Sketch map of territories of mockingbirds on the north coast of Hood Island, showing approximate boundaries (from observations of feeding, chasing, etc.) and sites of observed Dances.

Dance. However, the Nelsons saw two Dances and other territorial behavior in the seabird colonies on Punta Suarez. Of about 20 mockingbirds that clustered at my feet to drink from a small can of water, I marked four and subsequently saw some of these up to half a mile from the marking site.

On Tower Island Dancing by *N. parvulus* was seen on several occasions, once between two birds (one, at least, a songster) immediately following a fight (the only fight that I saw). Four bands, of two to four individuals each, could be distinguished in the area near our camp at Darwin Bay.

On Indefatigable Island the mockingbirds (N. parvulus) are less numerous and less tame than on Hood; some of them were nesting during the period November 1962–April 1963. Dances were apparently limited to pairs and I never saw other birds attracted to the dancers as described by Venables for breeding mockingbirds on Chatham Island. Once I saw a recently fledged bird beg (unrewarded), sing briefly, and feed the next brood of its parents in the nest.

On Champion Islet there were few N. trifasciatus; I saw Dances on four occasions, but noted no clear differences from the Dances of macdonaldi.

Other behavior.—Not only are the mockingbirds of Hood fearless of man but they also showed no fear of a hawk (Buteo galapagoensis) while it perched

in the camp. They neither mobbed the hawk nor fled from it, but did show interest in it and approached within about ten yards while it fed on a lizard (Tropidurus). At first sight this lack of fear seems remarkable since D. W. Snow found a hawk's nest with young near Punta Suarez (Hood) at which the food remains were mainly mockingbirds. J. B. Nelson (in litt.) observed that the mockingbirds "have a special 'chirrup' alarm call which immediately elicits a striking fleeing response from every mockingbird within hearing. We saw it several times when a hawk flew over." (Italics added.) I heard a few "chirrups" when the hawk flew short distances but saw no directed fleeing. At no time did the hawk fly overhead. Finches (Geospiza conirostris and G. fuliginosa) watched the perched hawk intently and made "tink" calls when it was on the ground amongst bushes. The doves (Nesopelia) appeared more alarmed. Several snakes (Dromicus) appeared in the camp and elicited immediate interest from the mockingbirds, which followed them and usually made a characteristic churring, chattering note.

Sunbathing occurred quite frequently, especially among the lower members of the band. Sometimes the bird would bend forward and fluff its back feathers but more usually it would lean to one side, raise the upper wing, and fluff the flank and back feathers while twisting the head and closing the nictitating membrane. Apparently identical movements were seen during three light misty showers.

DISCUSSION

Territory and dancing in two other mockingbird species.—Mimus polyglottos of North America defends a pair territory in the spring and summer and both sexes may defend individual or joint winter territories (Laskey, 1962) but the pattern of exclusive breeding territories is distorted by the presence of a rich source of food (e.g., a feeding station at a house) to which territorial birds come from up to ¼ mile but show no lasting territorial behavior near the feeding place (Michener, 1951). Dancing usually involves only two birds but Michener and Michener (1935) watched pairs opposing a new bird on several occasions. The Micheners' observations suggest that Dancing occurs during the establishment of the territories; my limited observations support this. Even when territories are being established, Dancing is a rarer display than the Dancing of Nesomimus, which occurs through a longer period.

In the arid coastal region of Ecuador the mockingbird, *Mimus longicaudatus*, is locally numerous and was breeding during my stay at Palmar during February and March 1963. They are markedly less aggressively territorial than *M. polyglottos* and respond less noisily to humans approaching nests with eggs or young. Marchant (1960) agrees that the territories may be less

strongly held than *M. polyglottos*, and suggests that there may be a tendency to polygamy. "Amicable associations of more than two birds were often noted in the breeding season, apart from the normal dry-season parties, and pairs forage for food for the young or building material far from their own territories, across intervening ones." I saw a few groups of three or four adult individuals but did not elucidate their breeding status; on one occasion I had a distant view of a Dance in which four of seven birds were involved.

The significance of collective territories in Nesomimus.—It is difficult to evaluate the ecological significance of the collective territories without a series of observations of marked birds extending through the breeding season. The clutch size of parvulus and melanotis is two or three (Venables, 1940), and macdonaldi is unlikely to differ markedly from this, so if the bands represent family parties they must be derived from several broods and have existed since the previous breeding season and subsequent postjuvenal molt. Breeding and molting may be dependent upon increased food, and thus upon rainfall, which occurs irregularly from December to March. The peak of breeding is probably about February; two broods per season are well known (Venables, 1940) and there might be more. Swarth (1931) suggests on the basis of 78 specimens, that the annual and postjuvenal molts are "accomplished by different individuals over a long period of time." But to explain the smaller bands inland it would be necessary to postulate a lower breeding success there. Alternatively the young birds from inland might move to the coast and form the large southern groups. Perhaps these southern birds are nonterritorial nonbreeders (with no nest-sites nearby) taking advantage of the rich food supply in the littoral zone or from the seabirds (cracked eggs, food scraps, etc.; Hatch, 1965), and are thus akin to Carrick's nonbreeding magpies (Carrick, 1963). If this is true, then the holding of collective territories may be linked with the control of population in the absence of many predators. It would be interesting to discover the fate of the different birds during the breeding season: do the bands split to form exclusive breeding territories and do the birds at the south coast move inland to breed although continuing to feed among the seabirds? These observations, admittedly scant, are reported in the hope of encouraging others to take advantage of the avifauna peculiar to the Galápagos Islands.

SUMMARY

Mockingbirds (Nesomimus macdonaldi) on part of Hood Island in the Galápagos were found in December 1962 to occupy collective territories within which they fed and roosted, which they defended against neighboring bands with a characteristic "Dance" similar to that of Mimus polyglottos. Within the band of four to ten birds there is an approximately linear hierarchy and up to three individuals were heard to sing. Elsewhere

on the island, amongst seabird colonies where there were no nesting sites, the band structure was apparently absent and it is suggested that these may be nonbreeding birds. Behavior of mockingbirds on other islands was not markedly different. Some observations are presented of other behavior patterns including responses to potential predators, and recognition of individual mockingbirds.

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Two new additions to the list of Life Members of the Wilson Ornithological Society are Mr. and Mrs. Stanley S. Dickerson of Somerville, New Jersey. The Dickerson's are well known among eastern ornithologists as enthusiastic bird-banders. Since 1953 they have banded over 43,000 birds of more than 170 species. For a number of years Mrs. Dickerson was the leader of the Island Beach, New Jersey, Operation Recovery Station, and more recently they have operated an OR station on Block

Island, Rhode Island. Mrs. Dickerson has been the long-time treasurer of the Eastern Bird Banding Association. Mr. Dickerson is a graduate of Rutgers University and Newark Law School, and is a practicing attorney. Mrs. Dickerson attended Duke University and Combs Conservatory. They are parents of four children, and include among their many activities membership in most of the ornithological and conservation organizations in this country, and a few abroad as well.